THE RESULTS OF INVESTIGATIONS OF THE ECOLOGY OF THE FLORIDIAN AND BAHAMAN SHOAL-WATER CORALS

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Received by the Academy, January 27, 1916

Many of the most important principles of coral ecology were long ago recognized and clearly formulated by Darwin and Dana. More recently Klunzinger, Pourtalès, Moseley, Alexander Agassiz, Verrill, Stanley, Gardiner, von Marenzeller, Duerden, Wood-Jones, and others have made important contributions.

The coral faunas which live in water less than 25 fathoms deep in coral-reef regions are separable into two subfaunas according to their ability for withstanding violently agitated water. These are (1) the strong, firmly attached, usually massive forms which can withstand breakers and the pounding of the surf; and (2) the weakly attached and branching forms which can survive only in quiet water. The forms requiring quiet water are further subdivisible according to their capacity to resist the deleterious effects of silt. A species of massive growth habit often will also live in quiet water. In some instances the same species of branching coral may be represented in both quiet and rough water, but the colonies in the rough water have shorter and stouter branches, responding to the environment by strengthening their skeletal structures. Massive, large, head-like corals, such as *Orbicella annularis*, form the strong frame-work of the reef while in the interspaces between the heads many colonies of species of smaller size grow and other organisms are present in greater or less abundance. *Acropora palmata*, a species of another growth habit, is an important reef builder in places. It forms ascending fronds which by the thickening of their basal portion become very strong. Two species which live in the quiet water on the flats behind the outer reefs or in the lagoons, are *Maeandra areolata*, which because of its small base of attachment could not remain fixed on the reef, and *Porites furcata*, which because of its fragile branches would be smashed to bits by the rough water of the outer reefs. These two species can exist where the bottom is muddy, as both possess the means necessary for ridding themselves of considerable quantities of silt. *Eusmilia fastigiata* is a species which has a fragile skeleton and requires quiet water, but as it can not endure much silt, it is restricted to areas where the bottom is cleaner. *Porites clavaria* illustrates responsive adaptation to environment, as it lives both on the reef and on the inner flats. The branches of the colonies in the former habitat are

short and stumpy or the colony may be almost massive in growth form, while in quiet water the branches may be decidedly elongated.

The depth to which the more massive forms extend is between 18 and 31 meters, 18 meters is usually about the maximum for vigorous growth, but some of the branching species extend to slightly greater depths. In general the lower depth of the shoal-water coral fauna of the West Indies is about 37 meters, approximating conditions in the Pacific. The precise cause of the limit in depth has not been determined. Each of several possible factors will be discussed.

All the corals with which I have experimented possess the capacity of removing a certain amount of sediment from their surfaces. This is affected by the nonnutrient particles becoming imbedded in mucus and by cilia removing the mucus and the particles from the surface of the tissue. The capacity for cleaning their surfaces varies according to the species, it being lowest among those corals which are most important on the outer reefs—it is low in *Orbicella annularia* and high in *Maeandra areolata*. Some corals, as *Siderastrea radians*, can endure having their surfaces covered with silt for some time. This coral seems to secrete a layer of mucus which lifts the silt above the tissue surfaces and thereby protects them. The branching form of many corals prevents sediment settling on them faster than it can be removed. However, as any coral will be killed by actual burial beneath sediment, corals can not live where sedimentation is rapid; and as sediment accumulates in areas deeper than the base of strong wave action or where currents are weak, it is a factor in limiting the depth to which the littoral fauna can extend.

The mechanism of corals for catching food are as follows: (1) The ectodermal surface is beset with nematocysts, which occur on the tentacles, the oral disk, the column wall, including its downward extension called the edge-zone, and also on the margin of the mesenterial filaments. (2) The entire ectodermal surface is ciliate, the cilia in response to certain stimuli beating toward the oral apertures; in response to others, beating toward the periphery. (3) The outer surface secretes mucus in which particles may be embedded, the mucus moving under the influence of the beat of the cilia toward the oral apertures or toward the periphery, according to the nature of the response to the stimulation. (4) The tentacles are active and effective in capturing food. (5) The mesenterial filaments, which in many species of corals can be extruded through the column walls, in some instances capture food.

Many different kinds of food were offered corals, but they took only animal food; they are entirely carnivorous. The following experiment was tried many times: A piece of diatom mat was placed on one side

of the oral disk and a piece of crab meat on the other. Invariably the crab meat was seized and swallowed; while the diatoms induced no reaction except ultimately to be removed from the surface. No kind of purely vegetable food was taken by any one of the numerous species investigated. However, pieces of plants coated with small animals or soaked in meat juice will be swallowed, and later the vegetal matter ejected.

As the food of corals is purely animal plankton, a decrease in the amount of this food-supply with increasing depth would limit the downward distribution of the shoal water forms, but as I do not know of any quantitative estimates of the amount of animal plankton above and below 20 fathoms in coral reef areas, there is no basis for a positive opinion.

The relation of corals to light was studied. Specimens of 17 species were put into a darkened, light-proof live-car. One of the number was dead at the end of 14 days; 3 others were dead at the end of 28 days; while 11 species survived at the end of 43 days. However, all had become pale, some even colorless, or otherwise showed abnormalities. A natural experiment, which appears conclusive, is afforded by Fort Jefferson wharf. Here corals thrive on all the outer piers where the light is strong but there are none on the central piers where there is perpetual shade. It therefore seems to me that strong light is essential for the vigorous growth of shoal water corals.

Another factor is temperature. Dr. Mayer conducted a series of experiments to ascertain the higher and lower limits of temperature which the common corals around the Tortugas can endure. These indicate that a lowering of the temperature to 13.9°C. would exterminate the principal Florida reef corals, while the most important inner flat corals would survive. He obtained similar results on the corals around Murray Island, Australia.

Dr. H. F. Moore of the U. S. Bureau of Fisheries has communicated to me temperature records made at lighthouses along the Florida reef. These show that vigorous reefs will endure a temperature as low as 18.15° C., the minimum at Carysfort light between 1879 and 1899; but at Fowey Rock, where the minimum drops to 15.6°C. although there are some corals, there is no thriving reef. The species found at the north end of the reef line are those which Dr. Mayer's experiments showed capable of withstanding the lowest temperature. The temperature records for the reef line indicate 18.15°C. as the minimum temperature which a reef will survive—this is 1.85°C. lower than the figure given by Dana. It is not probable that a reef could withstand a continuous

temperature so low as this. Wherever the depth of water is great enough to lower the bottom temperature below 18.15°C., more probably about 21°C., reef corals will not live. This temperature appears to be attained around the Hawaiian Islands within a depth of 183 meters. According to Agassiz's *Three Cruises of the Blake* the bottom temperature in the Gulf of Mexico and Caribbean Sea is usually too low for the growth of reef corals at a depth of 183 meters, and in places it is too low at a depth of 87 meters. Although the possibility of control of the lower bathymetric limit of reef-building corals by decrease in temperature with increasing depth has not been adequately investigated, it appears safe to say that reef corals are usually, if not always, confined by temperature to water less than 180 meters deep.

The four possible factors which tend to limit the downward extent of reef forming corals are as follows: (1) effect of sediment, (2) decrease in supply of small animal plankton, (3) decrease in intensity of light, (4) lowering of the temperature.

The relations of corals to salinity will now be considered. The average salinity of the Tortugas water according to Dole is 36.01‰. Seventeen species of the Tortugas corals were kept in a large tank of water with a salinity of 18.28‰ for 24 hours. All were damaged or killed except *Maeandra areolata, Siderastrea radians*, and *Porites astreoides*; but no specimen of 16 species showed any evidence of harm after remaining 48 hours in water of a salinity of 27.87‰. Apparently corals would not be hurt if the salinity of the ocean were reduced to about 80% of its present salinity. Although I did not experiment with concentrated sea-water, the studies made by Goldforb and others on the effect of concentrated and diluted sea-water on regeneration in hydroids and in the *Cassiopea* are here pertinent. The combined results of the experiments are in accord with the deductions made by oceanographers and geologists from other data, viz., the ocean is becoming more salt, and it appears that marine organisms are now living in an environment which is considerably below the optimum condition for their existence.

In order to ascertain the amount of atmospheric exposure corals would endure, experiments were made on 16 species, any of which will endure exposure on a glass plate in the shade for half an hour without apparent damage; nearly all will stand an hour without harm, while some will stand 4 hours' exposure under the conditions stated. *Favia fragum, Porites clavaria*, and *Porites astreoides* have the greatest capacity for withstanding atmospheric exposure, while that of *Maeandra areolata* and *Siderastrea radians* is almost as great. A number of species withstood exposure on a glass plate in the sun for 1½ hours, the specimens

being badly damaged, but not entirely killed. Although not precisely true, in general the ability to withstand atmospheric exposure is a function of the porosity of the skeleton, the species with the more porous, surviving longer than those with the denser skeletons.

The conditions necessary for vigorous coral reef development may be summarized as follows: (1) Depth of water, maximum, about 45 meters; (2) bottom firm or rocky, without silty deposits; (3) water circulating, at times strongly agitated; (4) an abundant supply of small animal plankton; (5) strong light; (6) temperature, annual minimum not below 18°C.; (7) salinity between about 27‰ and about 38‰.

In the experiments on rearing corals, the planulae were removed with a pipette from the vessel containing the parent colony to a jar on the bottom of which was a terra-cotta disk. Although the planulae will live a long time, even settle in stale water, kept at the proper salinity, it is better to change the water at least once a day. To change the water, siphons were used, a fine-mesh bolting cloth bag having been tied on the end within the jar, so as to prevent the escape of the planulae; while clean water was added through siphons from jars placed at a higher level.

Because of its bearing on the possibility of the distribution of coral species by oceanic currents, it is highly important to know the duration of the free-swimming larval stage. Observations were made on four species. The range was from 2 to 23 days. Should an ocean current have a velocity of 3 knots per hour, in 23 days planulae might be carried 1656 knots; at 2 knots per hour, 1104 knots; at 1 knot per hour, 552 knots. It is known that every species of shoal water coral in the Bermudas is found in Florida and the West Indies; while not only is the Hawaiian fauna Indo-Pacific in its facies, but several of the species (at least 4) also occur on the east coast of Africa or in the Red Sea. I seriously doubt any part of the Hawaiian fauna being peculiar to those Islands. The clue to the cause of the wide distribution of living coral species is given by the possibly long duration of the free-swimming larval stage.

The growth rate of corals was determined by planting planulae which attached themselves in the laboratory, by measuring colonies, from planulae which settled on collectors in a known season, by measuring colonies cemented to disks and fixed on the heads of stakes driven into the sea-bottom, and by measuring colonies naturally attached. The plantings around the Tortugas were made on the reef off Loggerhead Key and on the outside of Fort Jefferson moat wall, while records were made on colonies growing naturally attached at the two stations men-

tioned, on the piers of Fort Jefferson wharf, and in Fort Jefferson moat. The observations in the Bahamas were made on artificially planted and naturally attached colonies at the east end of South Bight, Andros Island. The Florida corals were measured annually; those in the Bahamas were measured in 1912 and again in 1914. The average growth rate for each species at each station has been computed. The size of the colonies of all species of corals seems limited, but some attain large dimensions, 2 to 3 meters or even more in diameter, and nearly as much in height, while other species are adult when a diameter of 35 to 50 mm. has been reached. *Favia fragum* and *Maeandra areolata* are instances of species which grow relatively rapidly for the first 2 to 4 years, after which they grow more slowly. *Orbicella annularis* and *Maeandra strigosa* are not so limited in size. Branching corals grow more rapidly than massive species; while of the former, the growth rate of species with perforate, loose-textured skeletons is more rapid than that of species with dense skeletons. In general the more massive and the denser the corallum, the slower the growth; while the more ramose and the more porous the skeleton, the more rapid the growth.

There is no average growth rate for corals generally speaking, as growth rate varies from species to species, and varies for the same species according to local environmental conditions. Here it may be said a colony of species of reef coral in a lagoon, if protected from sediment, may grow more rapidly than a colony of the same species does on the reef. The limitation of reef corals so largely to the outer edges of platforms is determined primarily by purity of water, i.e., freedom from silt, and by the more uniform temperature.

In order to estimate the rate at which a reef will grow, the upward growth rate of the true reef-forming species must be taken. The upward growth rate of *Orbicella annularis*, the principal builder of the Pleistocene and living reefs in Florida and the West Indies, is from 5 to 7 mm. per year, according to station. At 6 mm. per year, it would form a reef 150 feet thick in 7620 years; at 7 mm. per year it would build the same thickness of rock in 6531 years. *Acropora palmata*, which grows more rapidly, might build a similar thickness in 1800 years. The growth of corals in the Pacific appears to be more rapid and according to Stanley Gardiner they might build a reef 150 feet thick in 1000 years. The investigation of the growth rate of corals shows that any known living coral-reef might have formed since the disappearance of the last continental ice sheets.

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